Mechanosensory hairs in bumble bees (*Bombus terrestris)* detect weak electric fields

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Bumble bees (*Bombus terrestris*) use information from surrounding electric fields to make foraging decisions. Electro-reception in air, a non-conductive medium, is a recently discovered sensory capacity of insects, yet the sensory mechanisms remain elusive. Here, we investigate two putative electric field sensors; antennae and mechanosensory hairs. Examining their mechanical and neural response, we show that electric fields cause deflections in both antennae and hairs. Hairs respond with a greater median velocity, displacement and angular displacement than antennae. Extracellular recordings from the antennae do not show any electrophysiological correlates to these mechanical deflections. In contrast, hair deflections in response to an electric field elicited neural activity. Mechanical deflections of both hairs and antennae increase with the electric charge carried by the bumble bee. From this evidence, we conclude that sensory hairs are a site of electro-reception in the bumble bee.

Electric Fields | Bees | Behaviour | Sensory Biology

Introduction:

Electro-reception is common in aquatic animals. First discovered in sharks (1), electro-reception has also been found in rays (2), amphibians (3), teleost fish (4, 5), dolphins (6), platypuses (7), and echidnas (8), which use electrosensory organs in their snout to detect prey in wet soil.

The first specialised electrosensory structures discovered were the "ampullae di Lorenzini" (9). Ampullae are small tubular cavities containing an electrolytic jelly (2), which maintains the same electric potential as the water immediately adjacent. In sharks and rays, differences in electric potential between the inside of the animal and the jelly are transduced by epithelial cells (10), where negative deviations in potential are excitatory whilst positive ones are inhibitory (11). Teleost fish have independently evolved electroreceptors that are excited by positive voltages and inhibited by negative voltages (11). This general mechanism for electro-reception has evolved independently in several animal lineages (12, 13).

Ampullary electro-reception requires the presence of an electrically conductive medium. Even in terrestrial animals such as the platypus and echidna, electro-receptive organs need to be submerged in water, or surrounded by damp or humid substrates in order to function (7, 8). In contrast, bees detect weak electric fields in dry air, an electrically insulating medium. Bumble bees detect the presence of floral static electric fields (14) and honey bees detect oscillating fields associated with their waggle dance (15). In air, ampullary electroreceptors are ineffective due to an absence of conductive medium between the sensory organ and the environment. We thus investigate the possibility that electric fields instead exert forces on charged, mechanosensory structures on the bee: hairs and antennae.

To investigate electro-reception in air, we use non-contact laser Doppler vibration measurements and electrophysiology. We test two hypotheses: First, bumble bees use their antennae to detect electric fields. This is supported by evidence that honey bee antennae deflect in response to electric fields analogous to those produced by conspecifics performing the waggle-dance (15). Second, bumble bees use mechanosensory hairs to detect electric fields. In support of that hypothesis is the rich literature on arthropod sensory hairs detecting small forces associated with fluid flow and sound particle velocity (16). We find that electric fields of ecologically relevant magnitudes cause motion in both the antennae and body hairs, but only hair motion elicits a commensurate neural response. From this we conclude that hairs are used by bumble bees to detect electric fields.

Results

Bumble bee hairs and antennae mechanically respond to electric fields

The motion of the antennae and sensory hairs in response to applied electric fields was measured using a laser Doppler vibrometer (LDV) (figure 1). LDV measures the vibrational velocity (v) of structures undergoing oscillations, which was transformed into displacement (x) and angular displacement (θ) (see SI). 'Displacement' is the absolute motion of the structure, whilst 'angular displacement' is the motion of the structure in relation to its length. Angular displacement is proportional to the strain on the mechanoreceptors innervating the joint, either at the flagellum-pedicel joint of the antenna (Johnston's organ) or the base of the hair.

Electro-mechanical responses to broad band electric field stimulation

A 400Vpp sinusoidal frequency sweep from 10Hz to 10kHz (sweep duration: 0.64s) was applied to a steel disk, 1cm from the hair or antenna. Alternating electric fields were used as they cause steady state velocity responses suitable for LDV. For

Significance

Electro-reception in terrestrial animals is poorly understood. In bumble bees, the mechanical response of filiform hairs in the presence of electric fields provides key evidence for electrosensitivity to ecologically-relevant electric fields. Mechanosensory hairs in arthropods have been shown to function as fluid flow or sound particle velocity receivers. The present work provides direct evidence for additional, non-exclusive, functionality involving electrical Coulomb-force coupling between distant charged objects and mechanosensory hairs. Thus, the sensory mechanism is proposed to rely on electromechanical coupling, whereby many light thin hairs serve the detection the electrical field surrounding a bumble bee approaching a flower. This finding prompts the possibility that other terrestrial animals use such sensory hairs to detect and respond to electric fields.

Reserved for Publication Footnotes

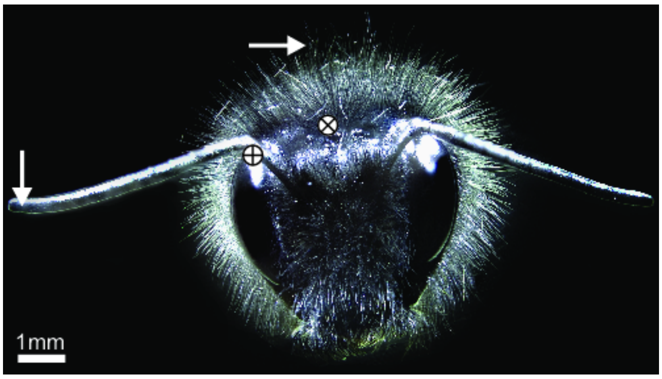

Fig. 1. Bumble bee covered in body hairs. White circles containing a plus (+) denote electrode insertion points in the antennae. White circles containing a cross (x) denote approximate electrode insertion points for hair recordings. White arrows show the laser focal position for hair and antennae LDV recordings.

each bee (N=10), the responses of two hairs and both antennae were recorded (figure 1), in both a charged and an uncharged preparation (see SI). The resonant frequency was the frequency of maximum response amplitude. The mean resonant frequency for hairs was 3.8 ± 0.2 kHz and 1.1 ± 0.3 kHz for antennae (table 1).

Hairs and antennae both move in response to electric fields. Hairs respond with significantly greater maximum and median velocity (v_{max}, v_{median}) than the antennae (figure 2a). The difference between maximum displacement (x_{max}) of hairs and antennae is not statistically significant, though hairs respond with significantly larger median displacement (x_{median}) (figure 2a). The tips of hairs and antennae move a similar absolute distance in response to electric fields at their respective resonant frequencies, though the hairs move more in response to spectrally broad electrical stimulation (figure 2b). Because hairs are much shorter than antennae, the maximum and median angular displacement (θ_{max}, θ_{median}) of hairs is significantly greater than that of antennae (table 1, figure 2c). The velocity of the hair is an order of magnitude greater than that of the antennae. Both hairs and antennae move like a stiff rod, pivoting the base where mechanosensory neurons are located. The absence of bending is revealed by the invariant phase response between the stimulus and the displacement at resonance (see SI: figure S3).

How sensitive is the electro-mechanical response?

To determine the minimum stimulus voltage generating a measurable mechanical response, spectrally pure sinusoidal voltages are applied to the stimulus delivery disk. To evaluate maximal sensitivity, stimuli were applied at the resonant frequency and at a second non-resonant frequency of the hair or antenna. The voltage at which the measured vibrational velocity is statistically distinguishable from thermal noise (U_{min}) is recorded for hairs and antennae in both charged and uncharged states.

Throughout the entire range of test conditions and stimulus voltages, the vibrational velocity of the hairs was an order of magnitude greater than that of the antennae (figure 3c, d). U_{min} was also lower for hairs than for antennae, indicating a higher sensitivity to electric fields (table 2). U_{min} for charged hairs was 25mV for both resonant and non-resonant stimuli. U_{min} for charged antennae was 500mV at resonance and 10V off resonance (between 20 and 400 times greater than the hair). Only when the bee's charge was deliberately set to zero, did the antennae respond to a lower voltage than the hair. In natural free flight situation, however, bees are only rarely found with zero charge (15, 17).

Minimum electric field strengths required to elicit electro-mechanical responses

To quantify the electric field associated with our stimuli and to evaluate its distance of action, finite element analysis (FEA) was used to compute field geometry and strength E. The computed field was evaluated at the location of the sensor (1cm axial distance from the disk) for various disk voltages. The minimum electric field strength (E_{min}) required to produce mechanical motion in charged hairs is 0.77 Vm^{-1} for resonant stimuli and 61 Vm^{-1} for non-resonant stimuli. For antennae, E_{min} is much higher (15.3 Vm^{-1} for resonant stimuli and 306 Vm^{-1} for non-resonant stimuli (table 2)).

When the disk is held at 30V, it produces an electric field of comparable magnitude to floral electric fields, and can be detected by bees on the wing (14). For a fixed disk voltage, the electric field strength E varies with distance r from disk as $E \propto r^{-2}$ (figure 4). The maximum distance at which the disk actuates the hair or antennae can then be used as a proxy for how relatively sensitive the structure is to an electric field. Accordingly, charged hairs can be actuated by a 30V disk at a distance of 7.1 to 55cm depending on stimulus frequency. Antennae are actuated at a maximum distance of 2.6 to 13cm depending on stimulus frequency (table 2, figure 4, 5). These distances of detection are consistent with the bumble bee's behavioural abilities reported by Clarke et al. (14).

The effect of electric charge on electro-mechanical responses

Bees accumulate charge during motion through their environment, (17; 14). A similar phenomenology likely applies to other flying or walking insects (18; 19). The bees used in this study, even in their charged state, carried less charge than they do *in vivo* (*in vivo* charge: 32±3pC (15); experimental charge: 4±1pC, N=10). Nevertheless, the effect of this small charge on the mechanical sensitivity of both hairs and antennae was pronounced. Charged bees respond with significantly greater amplitude than uncharged bees (paired T-tests between charged and uncharged preparations $p<0.01$ throughout). This corresponds to a 5 to 53 fold increase in electromechanical sensitivity, across all measurements, between bumble bees carrying no charge and those carrying one tenth of the charge of a free-flying bumble bee (table 1).

Electro-mechanical responses of hairs and antennae to DC electric fields

Hairs and antennae were stimulated with a 400V square pulse lasting 1 second. The onset of the electric field produces a transient velocity signal measured by the laser which was integrated with respect to time to give the change in position of the structure. This experiment was only performed on charged bees. The average displacement for antennae was 1.2 ± 0.4 µm. This is consistent with observations of the antennae in honey bees, which are displaced approximately 1 µm in response to 450 V, 40 Hz electric stimuli (15). The average displacement of the hairs was significantly lower at 0.14 ± 0.05 µm (paired T-test: $p<0.005$). The corresponding angular displacements were $(3.3 \pm 1) * 10^{-3}$ degrees for the antennae and $(3.7 \pm 0.01) * 10^{-2}$ degrees for the hairs. In response to the same static electric field, the angular deflection of the hair was 11 times greater than the angular deflection of the antenna (paired T-test: $p<0.001$ N = 10). If 400V is applied to a needle, which concentrates the electric field near the tip, the hair can be moved hundreds of microns, a motion large enough to be visible under the microscope (supplemental video 1).

Bumble bee hairs exhibit neural correlates to DC electric field stimulation

To determine whether the observed mechanical deflection is accompanied by a response from the nervous system, we measured the electrophysiological response of hairs and antennae to a 400V square pulse applied to a steel disc 1 cm away (figure 6a, 6b, 6c). All electrophysiological recordings were carried out on bees in their uncharged state, due to the necessity of grounding the bee to eliminate noise from the recording.

Table 1. Key results from laser Doppler vibrometry experiments. The 95th percentile and median values of velocity, displacement and angular displacement in response to 10Hz-10kHz sinusoidal electrical chirps at 400Vpp amplitude. Results from both charged and uncharged preparations. Asterisks show significance of difference between hair and antennae response under identical preparation and stimulation (T-test (paired): $p \leq 0.05$ (*); $p \leq 0.01$ (**); $p \leq 0.001$ (***); N=10).

		Charged			Uncharged		
		Hair	p	Antenna	Hair	p	Antenna
Velocity	95pctl	51.8 ± 8.3	***	4.9 ± 1.2	0.97 ± 0.1	***	0.31 ± 0.03
(μm/s)	Median	10.3 ± 3.1	**	0.71 ± 0.19	0.30 ± 0.04	**	0.16 ± 0.02
Disp.	95pctl	2.6 ± 0.5	n.s	1.2 ± 0.5	0.070 ± 0.01	n.s	0.077 ± 0.01
(nm)	Median	0.5 ± 0.1	**	0.026 ± 0.01	0.011 ± 0.002	**	0.005 ± 0.001
Ang Disp.	95pctl	13200 ± 270	***	61.7 ± 23	345 ± 34	***	3.84 ± 0.49
(deg x 10^{-9})	Median	2290 ± 670	***	1.28 ± 0.4	56.6 ± 11	***	0.24 ± 0.03

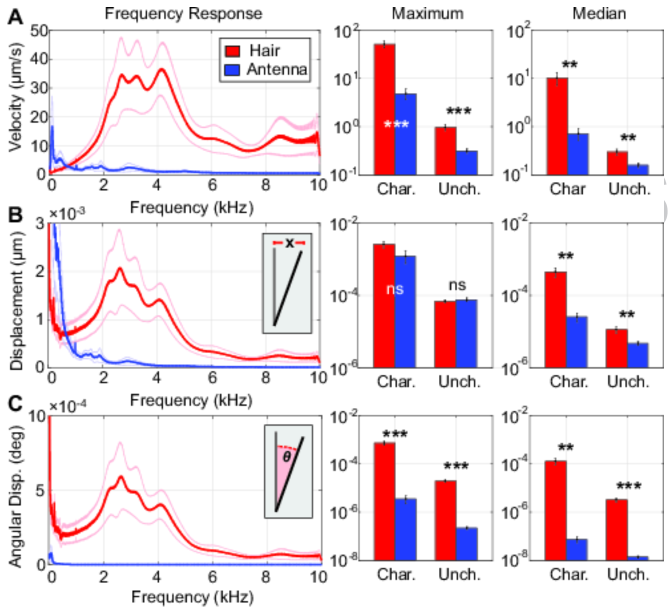

Fig. 2. Antenna (blue) and hair (red) motion in response to 10Hz-10kHz electrical chirps. Rows show the velocity (top), displacement (middle) and angular displacement (bottom). Columns show the response at each frequency (left), the amplitude of maximum response (middle) and the median response amplitude across all frequencies (right). Insets show a representation of the quantity being measured.

Bumble bee hairs (N=12) showed an increase in neural firing rate in response to the applied DC electric field (figure 6b, 6c). Some hairs had a background firing rate, while others were quiet before stimulus application. During the stimulus, the mean firing frequency of hairs was 5.1 times greater than the pre-stimulus firing rate (paired T-test: $p<10^{-6}$, N=14). In contrast, stimulation failed to increase firing frequency in the antennae (paired T-test: $p>.05$, N=14) (figure 6c). Dynamic stimulation at 140 Hz (N = 5) also failed to elicit an electrophysiological response from the antenna (see SI). In control recordings (figure 6e, 6f and supplementary information (SI)), however, the antenna responded to mechanical (air puffs) and olfactory (lavender oil) stimuli, showing the adequacy of the present electrophysiological preparation. These responses were consistent with previously reported antennal sensitivity to mechanical and olfactory stimulation (20).

Discussion:

From this evidence, we conclude that bumble bees use mechanosensitive hairs to detect electric fields. In honey bees (*Apis mellifera*), the antenna has been proposed to detect

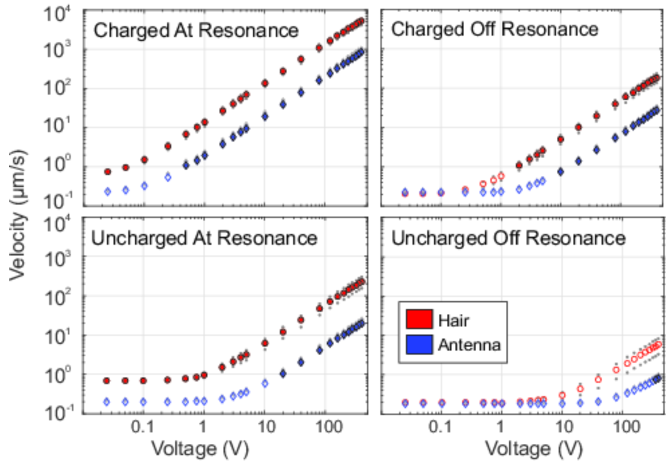

Fig. 3. Antenna (blue) and hair (red) mean velocity in response to oscillating electric fields at the resonant frequency of each structure (left) and at the frequency of median response (right) under charged (top) and uncharged (bottom) preparations. Grey dots show standard error of the mean. Filled shaped denote responses that were significantly larger than thermal noise. Unfilled shapes denote responses statistically indistinguishable from thermal noise.

Table 2. The minimum voltage on a disk 1cm away from a bumble bee required to produce a mechanical response (U_{min}), the electric field corresponding to this voltage (E_{min}) and the axial distance from a 30V disk at which electric field strength is equal to this value (D_{max}).

	Charged		Uncharged	
	Hair	Antenna	Hair	Antenna
V_{min} at resonance (V)	0.025	0.5	0.025	20
V_{min} off resonance (V)	2	10	400	360
E_{min} at resonance (Vm^{-1})	0.77	15	0.77	612
E_{min} off resonance (Vm^{-1})	61	306	12249	11024
D_{max} at resonance (cm)	55	13	55	1.6
D_{max} off resonance (cm)	7.1	2.6	0.1	0.6

electric fields, whereby Johnston's organ transduces mechanical deflections of the flagellum in response to an electric field analogous to that generated during a honey bee's waggle dance (15). Cockroach antennae have been shown to react to more intense electric fields, in the range of 8 to 10 kVm^{-1} (21). Our

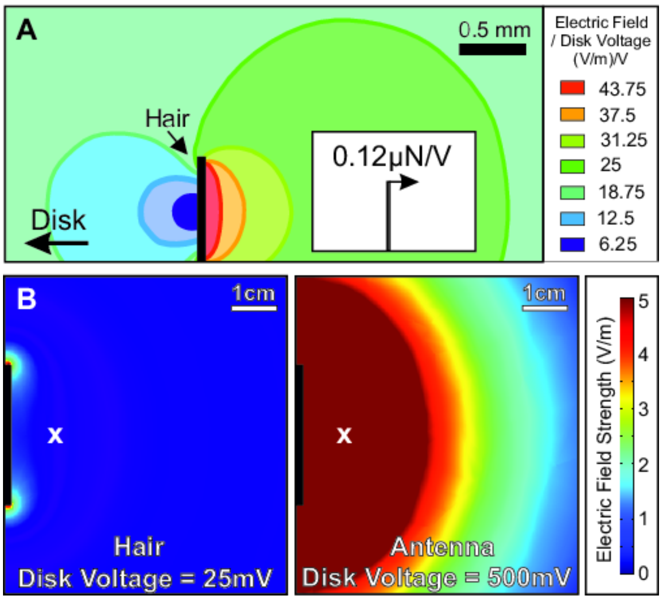

Fig. 4. (A) A finite element model of a bumble bee hair under an electric field produced by a steel disk 1 cm away. Electric field values are given per positive volt on the disk. Inset: the resultant projected force on the hair (0.12 µN per volt on the disk). (B) The simulated electric field due to the disk at 25mV (left) and 500mV (right), the minimum voltages which caused observable motion in the hairs and antennae respectively. The white x shows the position at which the hairs and antennae were located in the LDV experiments.

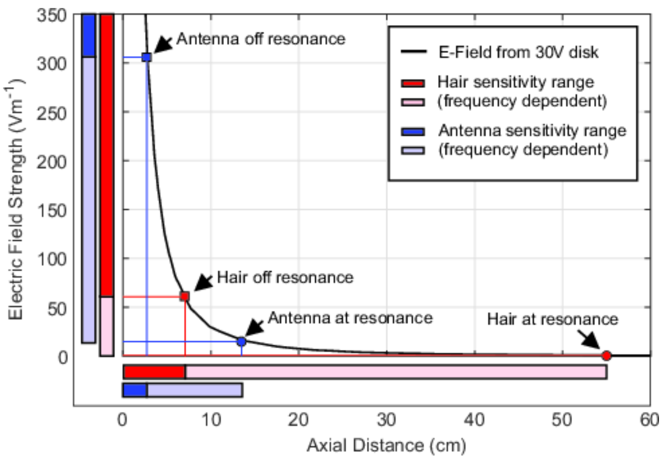

Fig. 5. : A finite element model of the stimulus delivery system showing electric field strength as a function of axial distance from 30mm steel disk held at 30V. The labelled points show the maximum distance of detection calculated for hairs (red) and antennae (blue) for resonant stimuli (circles) and non-resonant stimuli (squares). The bars on each axis represent the range of values of electric field and distance at which these structures show a mechanical response. The lighter area shows the difference between at-resonant and off-resonant stimulation, showing the responses within this range are dependent on frequency. The dark coloured areas of the bars show the range at which the structures respond at all frequencies.

similar experiments in bumble bees failed to demonstrate that antennae could respond to electric fields.

Mechanosensory hairs are common across the Phylum Arthropoda (16). These sensors typically have mechanical resonances between 100-500 Hz and react to vibrations from the wingbeats of approaching predators (22) and air currents (23, 24). In contrast, bumble bee hairs have a resonant frequency around 3.8 kHz, a result of low mass and high stiffness. Their rigid lever like motion within the socket resembles the acoustic

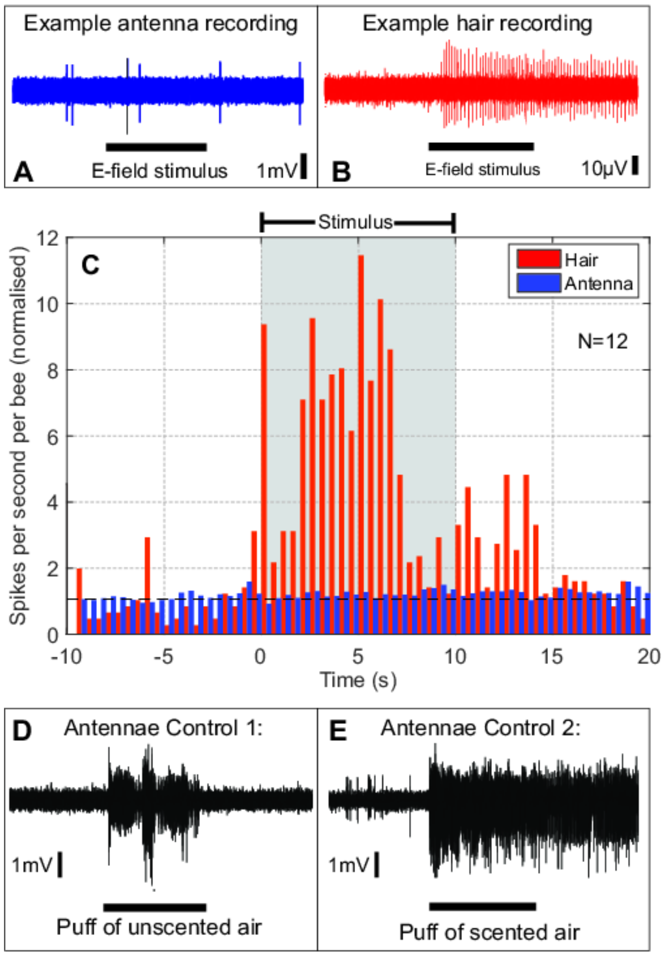

Fig. 6. The electrophysiological response to an electric field. (A, B): Example response of an antennae (blue) and a hair (red) to an electric field. (C) Plot showing the observed changes in firing rate of 12 antennae (blue) and 12 hairs (red) to an electric field stimulus (applied during the grey box). The value shown is the number of spikes per second, per bee, divided by the mean pre-stimulus spike rate. A value of 1 (dashed black line) indicates no change in spike rate. (D, E) two control stimuli applied to the antenna – puffs of unscented air (D) and a puff of scented air (E) demonstrate the lack of response of the antenna seen in (A) is not due to damage during the dissection.

particle velocity induced response of other mechanically sensitive hairs (25) and the feathery antennae of mosquitoes (26). Bumble bee hairs neurally respond to electrically induced deflections of 4×10^{-2} degrees (table 1), making them less sensitive than cricket filiform hairs, which respond to deflections of 2×10^{-2} degrees (27). Overall, electrosensory bumble bee hairs and mechanosensory hairs reported in other arthropods (16) are mechanically and neurophysiologically similar.

Some substantial differences exist in the biophysics of particle velocity (air movement) and electric field detection. For particle velocity detection, viscous coupling between stimulus and detector transfer energy into momentum of the hair. For electroreception in air, Coulumbic interactions couple the hair and the electric field, creating different mechanics. Notably, the boundary layer constraints inherent to particle velocity detection do not apply to electric forces. Particle velocity motion and electric field detection do apply a similar magnitude of deflection to hairs; with slow air currents causing cricket cercal hairs to deflect between $5*10^{-3}$ and $5*10^{-2}$ degrees (depending on the magnitude of the boundary layer and other effects; (28)), and DC electric fields deflecting bumble bee hairs by $4*10^{-2}$ degrees. The details of momentum transfer between the electric field and a charged hair (the electromechanical transfer function) are unknown, but will depend on the magnitude and distribution of charges along the hair. Forces generated by electric fields constitute a novel source of mechanical stimuli to arthropod hairs. Interestingly, both particle velocity and electric field stimuli can be generated simultaneously by a single source – such as a charged insect flapping its wings. *A priori*, both type of stimuli can act simultaneously on a single charged hair. This raises the possibility that particle velocity information and electrical information, and interactions between them, can be encoded by a single hair. The present study enables the formulation of the tantalizing hypothesis that, through the electromechanical sensitivity of hairs, electroreception is widespread in arthropods, fulfilling functions beyond the detection of floral electric fields.

Methods and Materials:

Laser Vibrometry

Bee Preparation: Bees were sacrificed with CO_2, and glued ventrally with cyanoacrylate to an electrically isolated piece of wood. They were attached to a mounting pin and placed in front of a laser Doppler vibrometer for measurement of antennal and hair vibration velocity (figure 1b). The bee was electrically charged by contact with a frictionally charged nylon ball-bearing, and left to settle for 10 minutes. After undergoing charging, bees carried an average of 4 ± 3 pC, where uncharged bees carried 0 ± 0.5 pC. The charge carried by a bumble bee *in vivo* is 32 ± 3 pC (14), hence in the experiments the charging below that measured in free flight. Charge stimuli used here are thus within the range of naturally occurring electrostatics. After initial measurements, the bee's charge was neutralised by application of a positive and negative ion beam (see SI). The stimulus regime was then repeated.

Vibrometry: Measurements of mechanical response of hairs and antennae to electric field stimuli were taken with a microscanning laser Doppler vibrometer (LDV) (Polytec PSV300) fitted with a close-up attachment. Data was acquired using an OFV5000 sensor head, digitised via an on-board data acquisition card (National Instruments PCI-4451) and subsequently analysed using PSV software (Polytec version 9.0). The target, laser source and stimulus delivery disk are placed on the same horizontal plane on an anti-vibration table (TMC 784-443-12R, 15 Centennial Drive, Peabody MA, 01960, USA) in an electrically isolated and sound-proofed booth (see SI: figure 1c).

Stimulus Regime: Electrical stimuli were delivered using an arbitrary function generator (Agilent 33120A) connected in series to a custom made high voltage amplifier. The stimulation electric field was generated by a 30 mm diameter steel disk connected to the high voltage amplifier by an earthed 50 Ohm BNC cable (as in (14)). A 400V periodic sweep from 10Hz – 10 kHz was applied to the disk. The frequency response and resonant frequency were recorded. To test for response amplitude relationship, a pure tone sine wave set at the resonant frequency was applied and the hair/antenna response recorded for incrementally decreasing stimulus amplitudes (400-380-360-…-0V). Stimulus amplitude was then increased back up to 400V to test each result for linearity. This was repeated for a second, off-resonant frequency that was chosen by identifying a frequency at which the amplitude of the response was equal to the median response amplitude across all frequencies. The bee was then prepared in its uncharged state and the whole regime was repeated. This entire procedure was repeated for both hairs and antennae.

Electrophysiology

Anesthetized bees were ventrally affixed to a post made of modelling clay (see SI). Extracellular recordings were made from both the antenna and the hair using electrolytically sharpened tungsten electrodes (see SI), using a national Instruments data acquisition card (NI 9172/9215) and custom built amplifier and LabVIEW 2011 to record the signal. For antennal recordings, the experimental electrode was inserted at the proximal end of the scape. The reference electrode was placed in the head, taking care not to place it near an ommatidium. For hair recordings, the experimental electrode was inserted in the basal socket. The reference electrode was placed in nearby cuticle.

Stimuli were delivered with the disk placed 1.0 cm from the bee in an identical arrangement to the LDV experiments. For all trials, there was an initial 10 seconds of no stimulation, followed by 10 seconds of electrical stimulation at 400V, followed by 10 seconds of no stimulation. For the antennae, additional control stimuli in the form of air puffs, scent, and AC electric fields were applied (see SI).

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